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ON THE ESTIMATION OF DISPERSAL AND MOVEMENT OF BIRDS

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Abstract. The estimation of dispersal and movement is important to evolutionary and population ecologists, as well as to wildlife managers. We review statistical methodology available to estimate movement probabilities. We begin with cases where individual birds can be marked and their movements estimated with the use of multisite capture-recapture methods. Movements can be monitored either directly, using telemetry, or by accounting for detection probability when conventional marks are used. When one or more sites are unobservable, telemetry, band recoveries, incidental observations, a closed- or open-population robust design, or partial determinism in movements can be used to estimate movement. When individuals cannot be marked, presence-absence data can be used to model changes in occupancy over time, providing indirect inferences about movement. Where abundance estimates over time are available for multiple sites, potential coupling of their dynamics can be investigated using linear cross-correlation or nonlinear dynamic tools.

Key words: capture-mark-recapture, estimation, occupancy, presence-absence, recoveries, spatial coupling, telemetry.

Sobre la Estimación de la Dispersión y el Movimiento de las Aves

Resumen. La estimación de la dispersión y el movimiento es importante para los ecólogos evolutivos y de poblaciones, así como también para los encargados del manejo de vida silvestre. Revisamos la metodología estadística disponible para estimar probabilidades de movimiento. Empezamos con casos donde aves individuales pueden ser marcadas y sus movimientos estimados con el uso de métodos de captura-repactura para múltiples sitios. Los movimientos pueden ser monitoreados ya sea directamente, usando telemetría o teniendo en cuenta las probabilidades de detección cuando se usan marcas convencionales. Cuando uno o más sitios no pueden ser observados, se puede estimar el movimiento usando telemetría, recuperación de anillos, observaciones circunstanciales, un diseño poblacional robusto cerrado o abierto, o determinismo parcial de los movimientos. Cuando los individuos no pueden ser marcados, se pueden usar datos de presencia-ausencia para modelar los cambios en el tiempo de la ocupación, brindando inferencias indirectas sobre los movimientos. Cuando las estimaciones de abundancia a lo largo del tiempo están disponibles para varios sitios, se puede investigar la interrelación potencial de sus dinámicas usando correlaciones cruzadas lineales o herramientas para dinámica no lineal.

INTRODUCTION

Dispersal is a topic of substantial interest to animal ecologists because of its importance to subjects ranging from evolution to population ecology and management (Clobert et al. 2001). Despite this interest, the study of animal dispersal was primarily descriptive until the 1990s. Early studies of marked animals documented that individuals marked in one location were sometimes recovered or recaptured at substantial distances from the site of release, but no inferences were generally made about the proportions of animals making such movements. The last decade has seen development of a number of methods permitting inferences about dispersal. Although this development has been reviewed (Nichols 1996, Nichols and Kaiser 1999, Bennetts et al. 2001), progress has been so rapid that these reviews do not adequately deal with all of the methods now available. Our intention here is not to provide detailed methodological descriptions, but to acquaint readers with the variety of estimation methods now available to study dispersal and animal movement. Here we devote special attention to recently developed methods.

There are many ways to classify any set of methods, and in this review we will base classification on the kinds of data for which the described methods were developed. The first such

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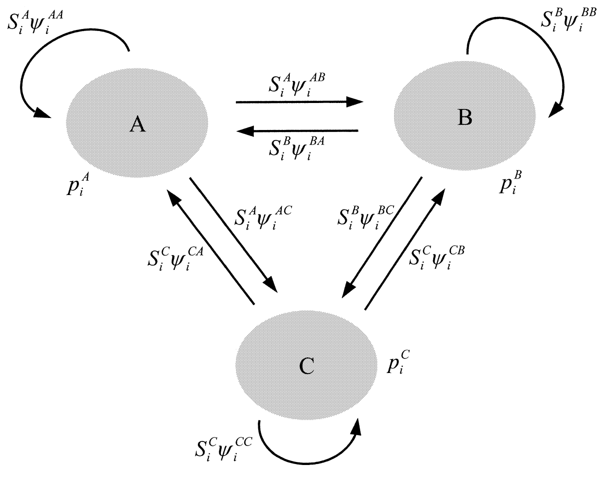

FIGURE 1. Diagram of movements of birds between study areas A, B, and C (e.g., breeding colonies, subpopulations), with associated probabilities of survival (S_i^r) for area r and movement from area r to area s (ψ_i^{rs}) for time i.

distinction is between methods based on multiple detections of marked animals (direct methods) and approaches based on detections of unmarked animals (indirect methods).

DIRECT METHODS: MARKED INDIVIDUALS

By capturing and applying a unique mark to a bird, we can track that individual's movements over time. There are three requirements for this tracking to be completely reliable, so that animal location can be determined at will. First, the animal must not move beyond the reach of whatever method is being used to track its movements. Second, the individual must be completely detectable (with probability 1.0), given that it is available. Third, if the individual dies or its mark fails (e.g., its band falls off), this must be apparent to the investigator. With the exception of many satellite telemetry and some radio-telemetry studies, at least one of these requirements is violated in most cases. Nevertheless, in most cases reliability can be partially or completely restored by collecting appropriate data and modeling the probability an individual moves to an unobservable location, or is not detected when it is present.

Several methods for encountering previously marked birds fall under the capture-mark-recapture (CMR) rubric. These include physical captures, radio- or satellite-based location of a transmitter, sightings for birds that have field-readable marks, and recoveries of bands from dead birds. We will review currently available CMR estimation methods that consider each of these data sources individually, and in combination.

Figure 1 describes a general form for our approach to considering bird movements. We partition time into discrete sampling periods (e.g., years) and space into discrete areas. For each period i and each area r we model the probability a bird survives (S_i^r), and, conditional on survival, the probability it moves to any given area s (ψ_i^{rs}). The convention of discrete time and space is not strictly required for completely reliable telemetry data, but is currently necessary when some birds can be present but not detected (i.e., probability of detection in area s in period $i < 1.0$). This structure can apply to many scenarios in the study of birds. Sites could be breeding colonies, where natal or breeding dispersal across years is of interest. Similarly, sites could be wintering or migration stopover areas. A seasonal model could also be developed, where transitions from breeding to wintering to migration stopover sites are tracked.

We will begin with the case where telemetry information is available for all areas and detection probability is perfect for each area and time period (i.e., $p_i^s = 1$). We will then consider where recapture or resighting information is available for each discrete sampling period for each area of interest, and then where recoveries are available for multiple areas. Finally, we will present options for estimation when one or more of the areas where members of a metapopulation are found is unobservable. Throughout we will refer the reader to available software for estimation.

TELEMETRY WITH PERFECT DETECTION PROBABILITY

When satellite transmitters are applied to birds, or where the range of a metapopulation during each time period does not extend beyond the reach of radios, and when each bird is detected with certainty and its status (live, dead, or failed radio) is known, it is straightforward to estimate movement probabilities. Consider the following encounter histories for a four-period study, with three areas A, B, and C: ABBC, 0CCC, BAAA, AAAA, ABBC, BCBB, ACCB, 000B, BABA, CCBB. History ABBC indicates the bird was banded at site A in period 1, then detected in area B for the next two periods, then in area C in period 4. History 0CCC indicates this bird was not banded until period 2, but then was detected in area C in each period thereafter. All 10 of these birds lived to the end of the study, so survival probability is estimated to be 1.0 for the duration of the study. In period 1 four birds were released in area A. Looking at what proportion of those were found in each area in period 2, 25% were found in area A (i.e., $\hat{\psi}_1^{AA} = 0.25$), 50% were found in area B ($\hat{\psi}_1^{AB} = 0.50$), and 25% were found in area C ($\hat{\psi}_1^{AC} = 0.25 = 1 - \hat{\psi}_1^{AA} - \hat{\psi}_1^{AB}$). These same estimates and their standard errors can be derived by using the multisite model features of programs MSSURVIV (Hines 1994), MARK (White and Burnham 1999), or M-SURGE (Choquet et al. 2004). Goodness of fit can be assessed in MSSURVIV or UCARE (Pradel et al. 2003, Choquet et al. 2004).

RECAPTURES, RESIGHTINGS, OR RECOVERIES WITH ALL STATES OBSERVABLE

It is rare in the absence of telemetry that $p_i^s = 1$ can be assumed. Arnason (1972, 1973) first developed CMR methods to address this problem for multiple sites, but they were not put to much use until Hestbeck et al. (1991) applied an extension of Arnason's approach to movement of Canada Geese (*Branta canadensis*) among wintering areas. Since then it has been applied in many cases, as reviewed by Nichols (1996), Nichols and Kaiser (1999), and Bennetts et al. (2001). Recent papers using these methods to estimate natal and breeding dispersal in birds include Blums, Nichols, Hines, et al. (2003) and Blums, Nichols, Lindberg, et al. (2003). We present two example detection histories, and associated conditional (on release) probabilities, for a three-period study with two areas, A and B:

$$\text{BAB} \qquad S_1^B \psi_1^{BA} p_2^A S_2^A \psi_2^{AB} p_3^B$$

$$\text{B0B} \qquad S_1^B [\psi_1^{BA} (1 - p_2^A) S_2^A \psi_2^{AB} + \psi_1^{BB} (1 - p_2^B) S_2^B \psi_2^{BB}] p_2^B$$

In the latter example the bird is not encountered in period 2. The two terms in brackets represent the probabilities associated with the two paths the bird might have taken (to area A in period 2 and then back to area B, or remaining in area B throughout) from release in period 1 to detection in period 3.

Although these models require that discrete locations be defined, continuous or discrete covariates can be assigned to these parameters. These can be individual covariates, such as the weight of the bird at banding, or group-based covariates such as climate variables. Nichols and Kendall (1995) pointed out the possibility of using distances between areas as a covariate

$$\psi_i^{AB} = \frac{e^{a+bd^{AB}}}{1 + e^{a+bd^{AB}}},$$

where the probability of moving from area A to B is a linear-logistic function (with intercept a and slope b) of the distance from area A to B (d^{AB}).

The model above assumes that movement probabilities are only a function of a bird's current location. Hestbeck et al. (1991) and Brownie et al. (1993) extended this to make movement probability for time period i conditional on a bird's location both at times i and $i - 1$. Estimates under this model can be obtained using program MSSURVIV and its fit can be assessed in MSSURVIV or UCARE, but Brownie et al. (1993) anticipated that in most cases achievable sample sizes would be insufficient to estimate the extra parameters of this extension with reasonable precision.

In some cases recaptures or resightings are not available, but recoveries of dead birds are. This is especially true with hunted birds, where hunters report recoveries of banded birds to a central repository such as the USGS Bird Banding Laboratory. Schwarz et al. (1988, 1993) developed methods for estimating probabilities of movement from area of banding to area of recovery. Kendall, Conn, and Hines (unpubl. manuscript) combined multisite recapture data with multisite recovery data to estimate movement among capture areas (e.g., breeding areas for waterfowl) and movement from capture area to recovery area (e.g., wintering areas for waterfowl). This model was implemented in program MSSRVrcv (Hines 2004).

UNOBSERVABLE SITES IN CAPTURE-MARK-RECAPTURE STUDIES

In many cases a marked bird will move to an area that is not subject to sampling effort. This might be due to inaccessibility, limited budget, or simply because that area is not known to the investigator. Such areas cause problems in tracking an animal's movements, even probabilistically. To understand this situation assume that Figure 1 represents the dynamics of a metapopulation of interest, but that there is insufficient budget to mark or observe birds in area B. Because no birds are released or observed in area B, movements to and from this area must be modeled based on supplemental or indirect information. Several recent publications have presented methods for estimating movement in the face of unobservable sites. To account for movement to or from unobservable sites these methods rely on either telemetry, universal band recoveries, secondary capture or sighting periods for each time period of interest, or partial determinism in transitions. We will discuss each of these in turn.

Telemetry. Powell et al. (2000) conducted a CMR study of Wood Thrush (*Hylocichla mustelina*) survival. Because they were concerned with movement out of the study area, which could bias survival estimates (Burnham 1993, Kendall et al. 1997), they applied radio harnesses to a subset of birds captured. They estimated movement probabilities in and out of the study area with telemetry, as described above. Combining this information with recapture information, they were able to correct for this movement in their survival analysis of thrushes marked without radios. This type of combined analysis could be conducted with program MARK, using the multistrata option with two groups (those marked with bands or radios, respectively), and assuming the same movement probabilities for those birds with and without radios.

Band recoveries and incidental sightings. In many cases birds can be assumed to spend at least some time each year in potentially observable sites. That is, if a bird dies during the year, it could be found and its band reported. Burnham (1993) used this assumption to estimate fidelity to a given area. He reminded his readers that the classic CMR survival estimator from the Cormack-Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) model estimates the probability a bird survives and remains faithful to its banding area (the complement of fidelity being permanent emigration). Because birds can be recovered anywhere, band recovery survival estimation (Brownie et al. 1985) yields estimates of true survival probability. Burnham (1993) combined recapture and recovery data in one model to yield an estimate of fidelity. Recent applications of this approach include Doherty et al. (2001), Frederiksen and Bregnballe (2000a, 2000b), Blums et al. (2002), and Frederiksen et al. (2002). This method is available in program MARK and could be implemented in M-SURGE. An assumption of this approach is that the relationship between survival probability for those that are or are not observable by capture or sighting is known (e.g., $S_i^U = S_i^O$), where *U, O* indicate unobservable (i.e., off the study area) or observable (i.e., study area) states, respectively.

Barker (1995, 1997) generalized Burnham's (1993) model to include incidental sightings of individuals. In this case it is assumed that an individual has some chance of being sighted and identified between standard sampling periods at some locations in its range. Under this assumption, these sightings can be viewed as recoveries where the animal is re-released. Of course, another assumption here is that birds are marked with field-readable marks, and that an observer knows where to report information. With this model Barker was able to estimate not only fidelity, but temporary Markovian movement outside the study area, with the additional assumption that movement probabilities are not time dependent.

Recent work has expanded on Burnham's (1993) model, permitting multiple capture or recovery states. Kendall, Conn, and Hines (unpubl. manuscript) allowed for multiple capture and recovery areas, and developed program MSSRVrcv (Hines 2004) as an estimation tool under these models. This approach permits an

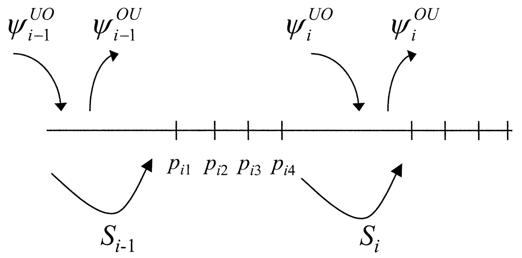

FIGURE 2. The closed population robust design for a single study site, where survival (S_i) and movement probabilities (ψ_i^{OU}, ψ_i^{UO}) between the observable study site (O) and unobservable areas off the study site (U) are modeled between primary periods (e.g., groups of four sampling occasions), and capture probabilities (p_{ij}) are modeled within each primary period.

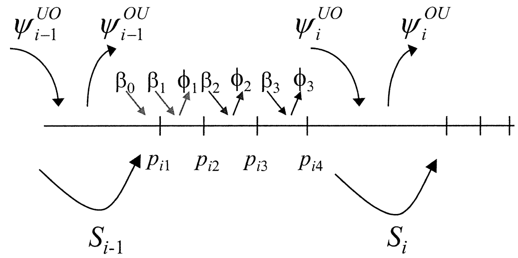

FIGURE 3. The open population robust design for a single study site, where survival (S_i) and movement probabilities (ψ_i^{OU}, ψ_i^{UO}) between the observable study site (O) and unobservable areas off the study site (U) are modeled between primary periods (e.g., groups of four sampling occasions), and capture (p_{ij}), arrival (β_{ij}) and departure ($1 - \phi_{ij}$) probabilities are modeled within each primary period.

unobservable capture site, but probabilities of movement from the unobservable site to any recovery site, and survival probability S_i^U cannot be estimated without additional restrictions. A known relationship between these parameters and their counterparts for observable sites must be assumed (e.g., equal survival probabilities as assumed above). Barker and White (unpubl. manuscript) considered multiple capture areas but did not partition recoveries into multiple sites. With an unobservable capture site under this model one must make an assumption only about S_i^U.

Robust designs and partial determinism. In many cases there is neither direct information on unobservable capture sites from telemetry, nor indirect information from band recoveries. One alternative means of drawing inferences about movement to unobservable sites is the use of the robust design (Pollock 1982). Under this design each primary sampling period is partitioned into multiple capture occasions, conducted over a relatively short period of time. Whereas in the face of movement to or from an unobservable site, the CJS estimator for detection probability tends to estimate a function of the product of detection probability and availability (i.e., $\psi_i^{OO}p_i^O$ and $\psi_i^{UO}p_i^O$), analysis of detection across capture occasions within a primary period permits unbiased estimation of p_i^O. Combining the between- and within-primary-period information permits estimation of ψ_i^{OO} and ψ_i^{UO} (Kendall et al. 1997).

There are two versions of the robust design and associated models that are pertinent to studies of bird movement. The first assumes closure of the study area to additions or deletions across sampling occasions within a primary period (Kendall et al. 1997, Fig. 2), although Kendall (1999) found that this approach is robust to certain violations of the closure assumption. Kendall and Nichols (1995) and Sedinger et al. (2001) used this approach to estimate the conditional breeding probabilities of Snow Geese (*Chen caerulescens*) and Black Brant (*Branta bernicla*), respectively, where only breeders were present. Lindberg et al. (2001) combined the band recovery approach of Burnham (1993) with the robust design approach of Kendall et al. (1997), to simultaneously estimate fidelity to a breeding population and conditional breeding probability for Canvasbacks (*Aythya valisineria*). Estimates under the closed robust design can be computed using programs RDSURVIV (Kendall and Hines 1999), or MARK (Kendall 2001).

The open robust design (Schwarz and Stobo 1997) relaxes the closure assumption so that each individual may enter and exit the study area once during each primary sampling period (Fig. 3). Entries and exits can be staggered throughout the primary period. In this case the arrival and departure process is modeled, in addition to detection probability, survival probability, and probability of movement. Using this design, Schwarz and Stobo (1997) modeled movement between years as completely random and assumed that within a year an animal could arrive and leave without being exposed to detection effort. Kendall and Bjorkland (2001) modeled between-year movement as Markovian and required that each individual using the study area in a given year be exposed to sampling effort (but not necessarily detected).

Open robust-design methods were first applied to breeding populations of seals and sea turtles. However, we believe they could be useful to the study of migration stopover of birds, such as in spring migration where individuals stop over long enough to acquire resources for the breeding grounds. In the case where only one stopover area is monitored, this approach could yield an estimate of conditional probability that an individual uses that stopover location in a particular year, in addition to providing estimates of survival probability, stopover time, etc. Open robust-design estimates can be computed using programs ORDSURVIV (Kendall and Bjorkland 2001) or MARK.

In many studies neither type of robust design was used to collect data, and in some cases the robust design is not practical. There are still cases where movement can be estimated when only one area is monitored. Fujiwara and Caswell (2002) found that if movement away from the study area is obligatory for at least two periods, and some sacrifice of time variation in parameters is reasonable, then movement can be estimated. Kendall and Nichols (2002) expanded on this and considered situations where movement away from the study area is obligatory for just one period, as well as where movement is not obligatory. They found that, practically speaking, partial determinism in movement, in addition to time constancy in some parameters, is required in order to estimate movement. Schaub et al. (2004) conducted a similar study and added the result that if parameters are shared between groups (e.g., sexes behave similarly), then movement can be estimated in some cases.

Lebreton et al. (2003), extending the method of Clobert et al. (1994), modeled the case where hatch-year birds are banded at multiple colonies, but become unobservable until they return somewhere to breed. By modeling the probability of first breeding as a function of age, and assuming that this probability asymptotes at some age, they were able to estimate natal and breeding dispersal using multistate models. They had neither the robust design nor assumed constancy in any additional parameters. They applied this method to three breeding colonies of Roseate Terns (*Sterna dougallii*).

INDIRECT METHODS: UNMARKED INDIVIDUALS

OCCUPANCY MODELING

Occupancy modeling is based on detection-nondetection (often termed "presence-absence") data. Such data involve visits by investigators to discrete units of the landscape. These units may be patches of suitable habitat, or the area of interest may be subdivided into discrete sample units (e.g., grid cells) to be sampled. Each unit is sampled at multiple times, with samples occurring at two temporal scales. Following the robust design terminology of Pollock (1982) for capture-recapture sampling, primary sampling periods are typically spaced sufficiently far apart in time that changes in occupancy are not rare. For example, the investigator might sample birds during the breeding season for several consecutive years, and these annual samples would define the primary sampling periods. Within each primary sampling occasion, the investigator returns to the site on multiple secondary sampling occasions that are closely spaced in time such that occupancy state is not expected to change.

This design yields detection history data that can be summarized as rows of ones and zeroes, denoting detection (1) and nondetection (0) at a sampling occasion. For example, consider a study with primary sampling occurring each year for 3 years, with two secondary samples per year. Consider the following detection history that might arise from such a study: 01 00 11. The species of interest was not detected at the first secondary sampling occasion of primary period 1, but was detected on the second secondary sampling occasion. The species was not detected at either visit during year 2, and was detected at both visits in year 3. We would like to model this history with parameters linked to the processes that gave rise to it.

Following Mackenzie et al. (2003), consider the following parameters:

p_{ij} = detection probability; probability that the species is detected at primary sampling occasion i, secondary occasion j, given presence during i;

ω_i = occupancy; probability that the species is present at primary sampling occasion i;

ε_i = local extinction probability; probability that the species is absent at primary period $i + 1$, given presence at i;

γ_i = local colonization probability; probability that the species is present at primary period $i + 1$, given absence at i.

Detection history 01 00 11 can now be modeled using these parameters as follows:

$$P(010011) = \omega_1(1 - p_{11})p_{12}[(1 - \varepsilon_1)(1 - p_{21})(1 - p_{22}) \times (1 - \varepsilon_2) + \varepsilon_1\gamma_2]p_{31}p_{32}.$$

The species is detected and hence present in the initial year, and the probability associated with this event is ω_1. The species was not detected in the first secondary period in year 1 (corresponding probability $1 - p_{11}$), but was detected in the second secondary period (p_{12}). The term in brackets is the sum of two components, reflecting the uncertainty associated with nondetection. The first component, $(1 - \varepsilon_1)(1 - p_{21})(1 - p_{22})(1 - \varepsilon_2)$, corresponds to the possibility that the species persisted and was present in year 2, went undetected, and persisted again to be present in year 3. The second component, $\varepsilon_1\gamma_2$, corresponds to the probability that the species went locally extinct between years 1 and 2, and then recolonized between years 2 and 3. The final detection parameters reflect detection in both secondary occasions of year 3. A probability expression such as the example above is associated with each possible detection history. The model likelihood is then constructed as the product of these expressions for the detection histories associated with all sites in the study. Maximum-likelihood estimates of the model parameters can then be obtained (Mackenzie et al. 2003). The colonization parameter, γ_i, reflects animal movement into the site, thus permitting inference about movement without the marking of individual animals. It is frequently hypothesized that site-specific colonization probabilities are functions of distance between the site and the nearest neighbor site or an associated source population (Hanski 1992, 1999). It is possible to formally test such ideas by embedding ultrastructural models (e.g., γ_i, as a linear-logistic function of distance to nearest neighbor) in the likelihoods described above.

These models are very new and have thus seen little use. An early version of the above model was used by Barbraud et al. (2003) to study colony site dynamics of Purple Herons (*Ardea purpurea*) in the Camargue wetlands of southern France. This species breeds in reedbeds, and such sites were surveyed by airplane twice each year for 20 years. Barbraud et al. (2003) identified three regions of the Camargue that differed with respect to habitat disturbance, in the form of reed harvesting. They hypothesized that local extinction probabilities of breeding colonies should be highest and most variable in the highly disturbed central region, and the occupancy modeling was consistent with this hypothesis. In addition, they hypothesized that local colonization probabilities in the eastern and western regions would be positive functions of local extinction probabilities in the central region. Modeling provided evidence for this hypothesis as well, yielding indirect evidence that birds were moving from the central region following disturbance to establish colonies in less-disturbed neighboring regions (Barbraud et al. 2003). This study provides an example of how occupancy modeling can be used to draw indirect inferences about animal movement.

TIME-SERIES ANALYSIS FOR SPATIAL COUPLING

In a previous review of methods for inference about dispersal, Nichols (1996) noted that abundance estimates from large-scale population survey data were sometimes used to draw inferences about animal movement. Assume that we have measured state variables such as population size at two nearby locations over a large number of years, generations, or other time intervals. From these data, we would like to draw inferences about the existence, strength, and even direction of coupling of the populations and their associated dynamics. A current approach used by ecologists would focus on synchrony in changes in abundance as estimated using linear cross-correlation analyses (Bjornstad et al. 1999, Koenig 1999). Positive correlations in abundance are interpreted as indicative of population synchrony, and such synchrony can result either from similar responses of the populations to environmental variation or from movement of animals between populations.

Cross-correlation is based on linear measures and addresses the existence of a specific kind of functional relationship between time series. However, small linear correlation does not imply that other (nonlinear) functional relationships do not exist (Pecora et al. 1997). The nonlinear dynamics that characterize at least some biological populations and communities (Schaffer 1985, Schaffer and Kot 1986, Hastings et al. 1993, Dennis et al. 1995) argue for the use of a more general approach to assessment of coupling. More general concepts than synchrony defined by linear cross-correlation are ''generalized synchrony'' and ''dynamical interdependence,'' which essentially means that two components come from the same system (Schiff et al. 1996, Pecora et al. 1997).

Investigating the possibility of dynamical interdependence between two time series involves first reconstructing the dynamics of the two systems, for example using attractor reconstruction via delay coordinates (Williams 1997, Kantz and Schreiber 1999), and then generally asking whether the attractors are related by a function with certain characteristics (e.g., continuity). Takens' (1981) theorem states that the trajectory of a dynamical system in phase space can be reconstructed from a time series of a single state variable from the system. Thus, a functional relationship must exist between attractors reconstructed from different state variables from the same system. The possibility of dynamical interdependence can be investigated by drawing inferences about the properties of potential functions relating two reconstructed attractors.

Two approaches from the field of nonlinear dynamics and based on attractor reconstruction have recently been used to investigate dynamical interdependence in an ecological model system, mutual prediction and continuity statistics (Nichols et al. 2005). Continuity statistics (Pecora et al. 1995, 1997) are used to assess the likelihood that the function relating two attractors is continuous. Mutual prediction (e.g., Schiff et al. 1996) is based on the idea that the existence of a functional relationship between two variables implies an ability to make predictions about one variable from knowledge of the other. In addition to being appropriate for general use with nonlinear systems, mutual prediction and continuity statistics also yield information about possible asymmetry in the relationship between the two time series. For example, it may be that dynamics in one location (e.g., a source, Pulliam 1988) are determinants of dynamics in another location, but not vice versa. Unlike linear cross-correlation, mutual prediction and continuity statistics reflect such asymmetries.

The potential utility of these approaches was investigated recently using output from a mathematical model (Pascual 1993) of a spatially distributed predator-prey system with diffusive movement of animals among patches and with patches showing a gradient in prey resource abundance (Nichols et al. 2005). The spatial gradient involved 100 discrete patches with different resource abundances, and the predator and prey abundances were ''sampled'' at each patch over a large number of time steps. Both continuity statistics and mutual prediction were able to detect dynamical interdependence and to provide evidence of the asymmetry of information flow in this system. These approaches have not yet been used with estimates of abundance (with their accompanying sampling variances) from actual survey data and with the short time series that are usually available. Thus, although we believe that these approaches hold promise, we also believe that they will likely require more work to assess appropriateness for actual ecological data.

OTHER INDIRECT METHODS

Other methods in addition to the two approaches described above have been suggested as means of drawing inferences about avian movement and dispersal based on single observations and encounters of individuals. One additional approach uses the facts that ratios of stable isotopes of naturally occurring elements vary in a characteristic way across the landscape, and that isotopic ratios in feather and other tissues of birds reflect those of the local environment in which the tissues were grown. Thus, feather samples of an individual bird from one time and place can be used to draw inferences about the bird's location at a previous time, permitting inferences about seasonal movement (Chamberlain et al. 1997, Hobson 1999, Webster et al. 2002). This methodological approach is discussed in other contributions to this issue (Hobson et al. 2004, Powell 2004).

Molecular genetics can also be used to draw inferences about avian movement. One approach to use of such data is similar to the approach based on isotopic signatures. If populations during one season are sampled at multiple points across the landscape, then it is possible to characterize them genetically. Genetic samples from individual birds at another season can then be used to draw inferences about their population membership, and hence their location, the previous season (e.g., Webster et al. 2002). Gene frequency data are used with assignment tests to make a probabilistic assignment of each sampled individual to a source population, thus permitting inference about movement (Waser and Strobeck 1998).

The other general approach to using molecular-genetic data to draw inferences about dispersal is based on population-genetic models for subdivided populations (Wright 1940, 1943, Rousset 1997, 1999, 2001). Subpopulations at two or more locations are sampled at a single time and the frequencies of neutral alleles are assessed using molecular-genetic techniques. Statistics such as F_{ST} are then computed to reflect the relative difference in genetic similarity (e.g., probability of identity in state of pairs of genes) within and between subpopulations (Rousset 2001). The basic idea is that less genetic similarity of subpopulations (i.e., greater differentiation) implies less dispersal. Measures of genetic similarity such as F_{ST} can then be obtained for subpopulations along a distance gradient and the relationship between similarity and distance used to estimate a function of density and dispersal under isolation by distance or island models (Rousset 2001). This basic approach has been widely discussed and has been frequently used to make qualitative statements about the magnitude of dispersal, but formal estimation of dispersal parameters based on this approach has been rare (but see Sumner et al. 2001). As with all attempts to deduce process from pattern, the approach is model dependent, and there are typically many different processes (e.g., model-parameter combinations) capable of producing any observed pattern in gene frequencies.

DISCUSSION

We have reviewed direct and indirect methods for estimating dispersal and other movements between discrete locations and across discrete periods of time. The most direct way to do this is to mark birds with reliable transmitters and simply track their movements as often as desired. However, expense, inaccessibility of birds, and size of transmitters prevent this approach from being the norm. Fortunately there are several alternatives to this approach, each with its advantages and disadvantages. Marking birds with leg bands in each area of interest is easier and less expensive per bird than telemetry. Detection probability can be modeled, but a larger sample size is required for the same precision as telemetry can provide, and unless color bands are used and reliable, individuals must be recaptured or recovered. The use of field-readable markers removes the need to recapture birds, but many of these markers (e.g., those that are plastic) tend to be less durable than metal leg bands and therefore some recapture is required to estimate marker loss. If sampling effort is withdrawn from a site or if alternative locations are not known, telemetry or the robust design can be used to estimate movement. However, the major problem here is that survival probability for unobservable and observable sites must be assumed equal. Without the robust design or telemetry, constancy of parameters over time is required to estimate movement of marked birds.

We have limited our consideration of dispersal to cases where birds occupy well-defined areas. Without completely reliable telemetry data, estimation of probability of dispersal to a point at any arbitrary distance from a source is problematic, due to the need to estimate differential detection probability among distances. If distance can be placed into discrete classes, and if birds remain faithful to the terminus of dispersal for a time, then multistate models as described above could be applied, where states are concentric circles around the source. Thomson et al. (2003) created such distance classes and, instead of estimating detection probabilities from multistate models, derived metrics reflecting relative detection probability from the number banded in each class and an index to abundance from atlas data.

When birds cannot be marked in sufficient numbers to study movement directly, indirect inferences about movement can be obtained from data on changes in occupancy or abundance through time. Different populations and locations sometimes have characteristic isotopic or genetic signatures, permitting inferences about source populations or locations of individuals sampled elsewhere. The degree of genetic differentiation between subpopulations can be assessed using molecular-genetic techniques and used to draw inferences about dispersal.

We believe that a promising area of future work will involve efforts to strengthen inferences by combining direct and indirect approaches to the study of movement. For example, Powell (2004) developed a model that combines the extra information from isotopic or other signatures with multistate capture-recapture data. MacKenzie and Nichols (2004) have begun to consider hybrid occupancy models that combine presence-absence data with observations of marked individuals at the surveyed locations. We believe that it should be possible to develop joint likelihoods that use both multistate capture-recapture data and multilocation genetic data (based on either an assignment test or relative differentiation approaches) to better estimate dispersal and related parameters. Even when using a direct, marked-animal approach with all sites observable, combining sources of data, such as secondary sighting sessions, telemetry, or recoveries, can increase the precision of estimates. It is especially advantageous to use "cost-free" information, such as recoveries of dead birds. Relatively user-friendly software exists with which to take advantage of these opportunities (e.g., programs MSSURVIV, MSSRVrcv, RDSURVIV, ORDSURVIV, MARK, and M-SURGE).

We encourage investigators to consider the state of the art we have summarized here when anticipating a study. First, the objectives of the study should be thought out carefully, including what parameters and questions are of biological interest, based on alternative hypotheses to be considered. Next, the state of the art in statistical methodology should be considered to determine if parameters of interest can be estimated with minimal bias (i.e., whether the assumptions can be approximately satisfied) and what kind of information needs to be collected to do so (e.g., Are there likely unobservable sites that would call for telemetry or the robust design? Can animals be captured at all?). If an appropriate method and software exist, then the study should be designed with this method and its assumptions in mind. If for some reason none of the available methods seem reasonable, the investigator should consult a statistician to see if some method could be modified to eliminate any potential problems. It is important to do this before the study is conducted because the solution to the problem might entail that ancillary data be collected. This interaction between practitioners and those who develop methods is how the state of the art is pushed forward and has been very productive to date.

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